

Reproducibility of results in phylogenetic analysis of mollusks: a reanalysis of the Taylor, Kantor, and Sysoev (1993) data set for conoidean gastropods

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Abstract: Reanalysis of the Taylor, Kantor, and Sysoev (1993) data set on conoidean gastropods failed to reproduce their results. Taylor *et al.* found more than 900 trees of length 189; reanalysis yielded 32,700 trees of length 187. The number of trees they found was limited by the memory available on the computer used for the analysis. The Taylor *et al.* consensus tree omitted the stated outgroup *Benthobia* (Pseudolividae); reanalysis including the outgroup yielded 3,149 trees of length 193, in all of which *Benthobia* fell within the ingroup. Strict and majority-rule consensus trees differed considerably in topology from those with *Benthobia* excluded. Reanalysis excluding the hypothetical ancestor, whose character states Taylor *et al.* determined in part by ingroup analysis, yielded additional topologies of consensus trees. Only eight of 38 clades in the Taylor *et al.* tree appeared in all three strict consensus trees; 17 clades were not supported by any of the majority rule consensus trees. All three majority-rule consensus trees did support the transfer to Conidae by Taylor *et al.* of the turrid subfamilies Clathurellinae, Conorbinae, Oenopotinae, Mangeliinae, Daphnellinae, and Taraninae. This clade, however, did not appear in two of the strict consensus trees, so support for it is equivocal.

Additional problems with the analysis include incorrect character mappings, use of characters primarily from one organ system, conflicts between text and data matrix, choice of taxa, and inclusion of data from taxa not included in the cladistic analysis in formulating the classification. The Taylor *et al.* data set does not support strong inferences about conoidean phylogeny, and there is not yet convincing evidence for abandoning the traditional classification of the group. Nonetheless, their data are an immensely valuable contribution to be built on as information about conoidean taxa, characters, organ systems, and outgroups accumulates.

Key words: cladistics, critique, Conoidea, anatomy, classification

Taylor, Kantor, and Sysoev (1993) presented an enormous body of anatomical data on conoidean gastropods, along with a phylogenetic analysis of their data. The phylogenetic tree they presented is reproduced here (Fig. 1), and will be referred to hereafter as the TKS tree, from the authors' initials. Based on their analysis, Taylor *et al.* introduced a revised classification of the superfamily Conoidea, which differs in a number of respects from the traditional classification that recognizes three families, Conidae, Turridae, and Terebridae. In particular, the turrid subfamilies Clathurellinae, Conorbinae, Oenopotinae, Mangeliinae, Daphnellinae, and Taraninae were transferred to Conidae, and Drilliidae, Pseudomelatomidae, and Strictispiridae, formerly subfamilies of Turridae, were elevated to familial status. Kohn and McLean (1994) critiqued the classification, but did not try to replicate the analysis. I attempted to reproduce the results of Taylor *et al.*, by reanalyzing their data, but was unable to do so. I found many more, and shorter trees, than they did, but because they gave insufficient detail about methods, it was difficult to tell why we had gotten different results.

There is always a danger that such a reanalysis will be viewed as a personal attack, although the debate between Bieler (1990) and Haszprunar (1990) over Haszprunar's (1988) "clado-evolutionary" classification of the Gastropoda shows that salutary results are possible. It was therefore with some trepidation that I approached Dr. John Taylor and Dr. Yuri Kantor, at a much later date than I should have (July 1998), to ask for clarification of their methods. They asked me to keep in mind that the analysis published in 1993 was performed in 1991, and that computing power and the sophistication of cladistic methods have both advanced considerably in the intervening seven years. With their cooperation, I have been able to include their comments about specific methodological points.

The question of whether the results of a phylogenetic analysis can be reproduced can be addressed at several levels. Given the same data and the same assumptions, can the results be replicated? How much do the results change with different assumptions? These are essentially questions of the mechanics of the analysis and its internal consistency. Equally important, but much harder to answer: would a

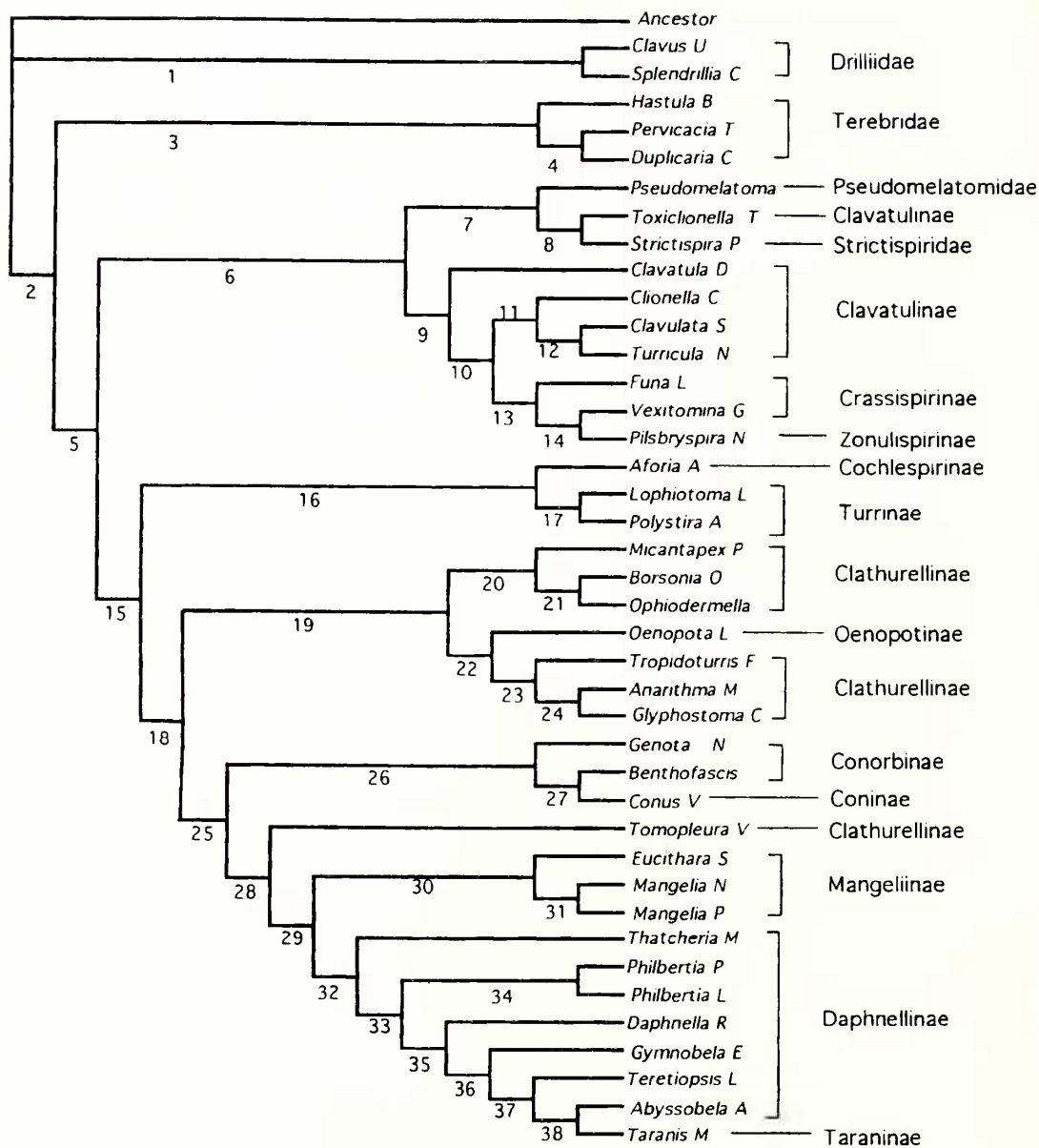


Fig. 1. TKS tree (50% majority-rule consensus tree from Taylor *et al.*, 1993: fig. 27). Names at the right show the new classification proposed by Taylor *et al.* Taxa are, in alphabetical order [with abbreviations in brackets]: *Abyssobela atoxica* Kantor & Sysoev, 1986 [*Abyssobela* A], *Aforia abyssalis* Sysoev & Kantor, 1987 [*Aforia* A], *Anarithma metula* (Hinds, 1843) [*Anarithma* M], Ancestor (hypothetical) outgroup, *Benthobia* outgroup, *Benthofascis biconica* (Hedley, 1903) [*Benthofascis*], *Borsonia ochraea* Thiele, 1925 [*Borsonia* O], *Clavatula caerulea* (Weinkauff, 1875) [*Clavatula* S; *Clavatula* C in Figs. 2-7], *C. diadema* Kiener, 1840 [*Clavatula* D], *Clavus unizonalis* (Lamarck, 1822) [*Clavus* U], *Clionella sinuata* (Born, 1778) [*Clionella* C], *Conus ventricosus* Gmelin, 1791 [*Conus* V], *Daphnella reeveana* (Deshayes, 1863) [*Daphnella* R], *Duplicaria colorata* Bratcher, 1988 [*Duplicaria* C], *Eucithara stromboides* (Reeve, 1846) [*Eucithara* S], *Funa latisinuata* (E. A. Smith, 1877) [*Funa* L], *Genota nicklesi* Knudsen, 1952 [*Genota* N], *Glyphostoma candidum* (Hinds, 1843) [*Glyphostoma* C], *Gymnobela emertoni* (Verrill and Smith, 1884) [*Gymnobela* E], *Hastula bacillus* (Deshayes, 1859) [*Hastula* B], *Lophiotoma leucotropis* (Adams and Reeve, 1850) [*Lophiotoma* L], *Mangelia nebula* (Montagu, 1803) [*Mangelia* N], *M. powisiana* (Dautzenberg, 1887) [*Mangelia* P], *Micantapex parengonius* Dell, 1956 [*Micantapex* P], *Oenopota levidensis* (Carpenter, 1864) [*Oenopota* L], *Ophiidermella inermis* (Hinds, 1843) [*Ophiidermella*], *Pervicacia tristis* (Deshayes, 1859) [*Pervicacia* T], *Philbertia linearis* (Montagu, 1803) [*Philbertia* L], *P. purpurea* (Montagu, 1803) [*Philbertia* P], *Pilsbryspira nymphia* (Pilsbry and Lowe, 1932) [*Pilsbryspira* N], *Polystira albida* (Perry, 1811) [*Polystira* A], *Pseudomelatomia penicillata* (Carpenter, 1864) [*Pseudomelatomia*], *Splendrillia chathamensis* Sysoev and Kantor, 1989 [*Splendrillia* C], *Strictispira paxillus* (Reeve, 1845) [*Strictispira* P], *Taranis moerchii* (Malm, 1863) [*Taranis* M], *Teretiopsis levicarinata* Kantor and Sysoev, 1989 [*Teretiopsis* L], *Thatcheria mirabilis* Angas, 1877 [*Thatcheria* M], *Tomopleura reevii* (C. B. Adams, 1850) [*Tomopleura* V], *Toxiclionella tumida* (Sowerby, 1870) [*Toxiclionella* T], *Tropidoturris fossata notialis* Kilburn, 1986 [*Tropidoturris* F], *Turricula nelliae spurius* (Hedley, 1922) [*Turricula* N], and *Vexitomina garrardi* (Laseron, 1954) [*Vexitomina* G]. [Reproduced with permission from the *Bulletin of the Natural History Museum (London)*.]

different data set, with different characters or different representative taxa, lead to similar phylogenetic inferences? In principle, it should, because there is only one true tree. If a phylogenetic analysis fails in either internal or external consistency, then it is not a good basis for classification. Because I am not an expert on conoidean anatomy, I have considered mainly the internal consistency of the Taylor *et al.* data set, rather than attempting to formulate a revised data set.

METHODS

Parsimony analysis was performed using PAUP 3.1.1 (Swofford and Begle, 1993) on an Apple Macintosh Centris 660AV computer. Taylor *et al.* used a Macintosh SE (pers. comm.) running PAUP 3.0. Three versions of the data set were studied: Analysis I, the original data matrix, exactly as presented by Taylor *et al.*; Analysis II, the original matrix excluding the outgroup *Benthobia* (Pseudolividae); and Analysis III, the original matrix excluding *Benthobia* and the hypothetical ancestor.

The heuristic search option of PAUP was used, with all characters unordered and equally weighted and search settings as follows: Random addition sequence (10 replicates); tree-bisection-reconnection branch-swapping performed; MULPARS in effect; steepest descent in effect; branches having maximum length zero collapsed to yield polytomies; topological constraints not enforced; trees unrooted; no trees in memory at start of run. Taylor *et al.* (1993: 152) also performed a heuristic search but did not state any of the settings. They were unclear about ordering of characters and did not mention weighting.

Strict and majority rule consensus trees were computed for the minimal trees for each set of taxa analyzed, along with partition lists showing clades found in one or more trees and their frequency of occurrence. MacClade 3.0.1 (Maddison and Maddison, 1992) was used to determine the length of particular trees, based on the original matrix, again with all characters unordered and equally weighted.

The following tree statistics were calculated: consistency index (CI), homoplasy index (HI), rescaled consistency index (RC), and retention index (RI).

RESULTS

Within each run, only one to four of ten replicates were completed before PAUP's maximum trees limit of 32,700 was reached, terminating the run. Therefore each analysis was run four times, with different random starting seeds to give different input orders of taxa. In some cases

tree memory was filled before the shortest trees were found. In particular, for Analysis II, some runs terminated with trees of length 188 and others with length 187 and for Analysis III some terminated at length 182, others at length 183. The results reported here are for the runs that yielded the greatest number of shortest trees; further analysis may yield yet shorter trees. In PAUP, when a run terminates because of the maximum tree limit, any non-minimal trees in memory (awaiting branch-swapping) are automatically discarded, so the number of most parsimonious trees found may be less 32,700. Search histories, which indicate discarded trees, are given in the figure captions of the strict consensus trees.

Analysis I

Reanalysis of the original data matrix yielded 3,149 trees of length 193. *Benthobia*, one of the designated outgroups, fell in the ingroup in 100% of the 3,149 trees (as seen from the partition list generated by PAUP), although its position was unresolved in the strict consensus tree (Fig. 2). In the majority rule consensus tree (Fig. 3), *Benthobia* grouped with *Duplicaria* and *Pervicacia* (Pervicaciinae) 82% of the time. Partition analysis showed that *Hastula* (Terebridae) fell as outgroup to all other conoideans in 37% of the trees, and *Conus* was outgroup in 3%. *Conus* plus *Hastula* was outgroup to the other conoideans in 16% (3% as a clade, 13% paraphyletic). Clades that these and the following consensus trees shared with the TKS tree (Fig. 1) are indicated in Table 1.

Analysis II

Reanalysis of the original matrix with *Benthobia* excluded yielded 32,700 trees of length 187. Figs. 4-5 show the strict and majority rule consensus trees. Partition analysis showed that *Conus* did not group within the turrids in 3% of these trees. *Clavus* plus *Splendrillia* fell as outgroup 43% of the time and the three terebrids fell as outgroup 15%. The TKS tree (Fig. 1), which also excluded *Benthobia*, is two steps longer, with length 189.

Analysis III

Reanalysis of the original matrix with *Benthobia* and the hypothetical ancestor excluded yielded 10,490 trees of length 182. Strict and majority rule consensus trees are shown in Figs. 6-7. Of interest here is that the strict consensus tree supports clade 18 of the TKS tree: Conidae including Clathurellinae, Conorbinae, Oenopotinae, Mangeliinae, Daphnellinae, and Taraninae.

DISCUSSION

Although the capability to make data and methods

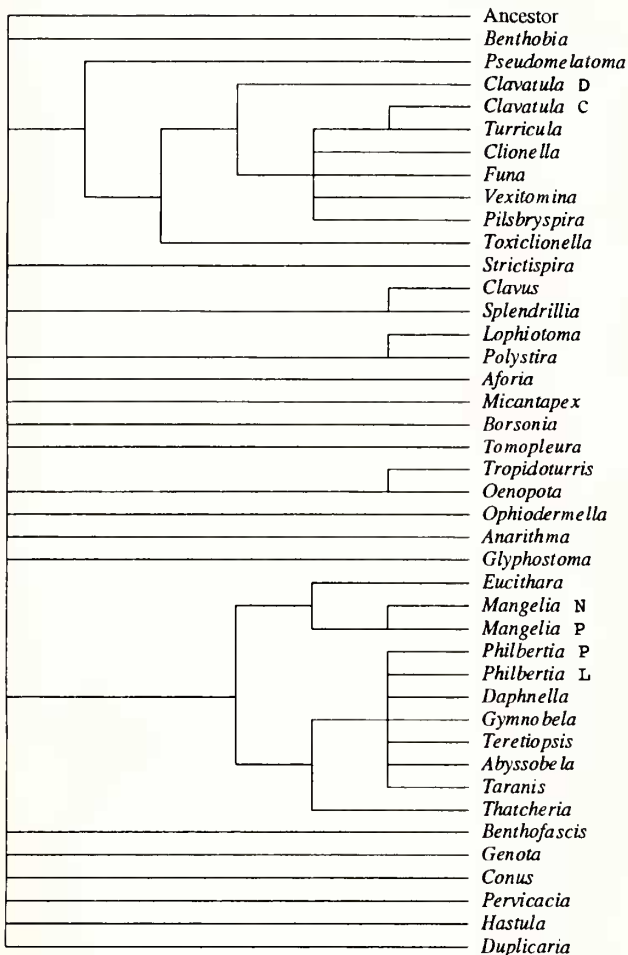


Fig. 2. Analysis I (including *Benthobia*); strict consensus of 3,149 trees, length 193, CI = 0.285, RI = 0.613, HI = 0.715, RC = 0.175. Search history: replicate 1 (seed = 357612083), 1,938 trees found (length = 193); replicate 2 (seed = 1222301227), 395 additional trees found (length = 193); replicate 3 (seed = 63292021), 816 additional trees found (length = 193); replicate 4 (seed = 1306497612), MAXTREES limit (32,700) hit while swapping on tree #11,591, 29,551 non-minimal trees (length = 194) discarded. Total number of rearrangements tried = 407682616, time used = 27:26:26.

explicit is one of the advantages of cladistics over traditional phylogenetic methods, some practitioners of cladistic methods do not take full advantage of this capability. For example Bieler (1990: 371) said of Haszprunar's (1988) "clado-evolutionary" classification of the Gastropoda: "The presentation of the data is incomplete and inconsistent. The analysis is not repeatable" and raised concerns about departure from standard cladistic practices. Reynolds (1997: 20) raised similar issues of "parsimony application and repeatability" in his reanalysis of Steiner's (1992) data set on Scaphopoda. My reanalysis of the conoidean data set further emphasizes that without full details of methods, assumptions, and limitations, results might not be replicable.

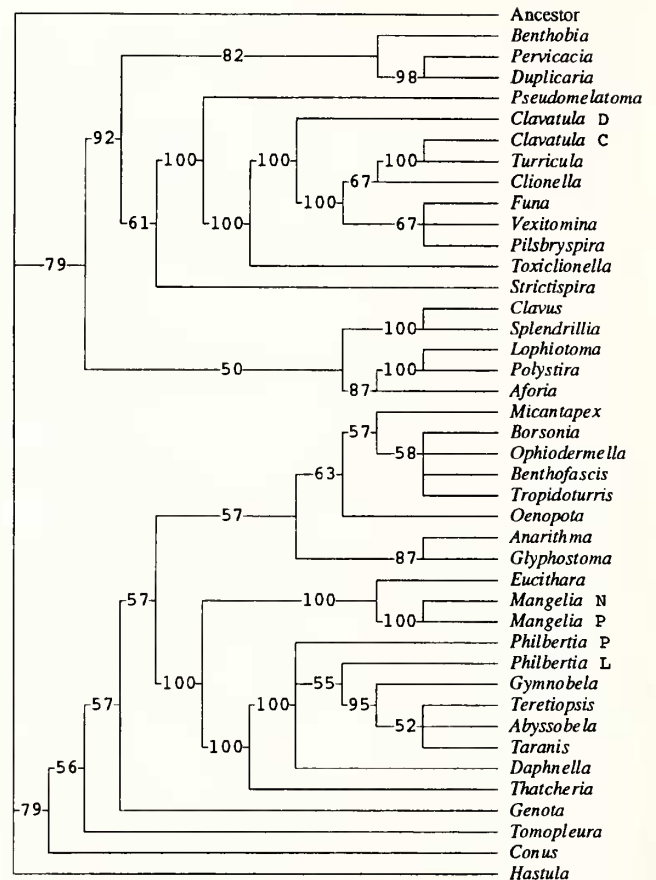


Fig. 3. Analysis I (including *Benthobia*); 50% majority-rule consensus of 3,149 trees of length 193.

I will show first that my Analysis II used the same data and the same assumptions as the analysis presented by Taylor *et al.* (1993), but got different results because of differences in computing power. I will then consider how different assumptions about outgroups, characters, taxa and classification might affect the reliability of the results.

RECONSTRUCTING THE METHODS

Data matrix and ordering of characters

From their stated methods, it is not clear whether Taylor *et al.* intended all characters to be unordered. On page 152, they flagged 18 characters as unordered: (2, 7, 23, 25-31, 33-38, 41-42), but in their table 2, only 15 characters were marked as unordered (2, 7, 23, 26-28, 30-31, 34-38, 40-41). Discrepancies involve characters 25, 29, 33, 40, and 42. All multistate characters were included on one list or the other, so presumably the published analysis was run with all characters unordered. This assumption is supported in that few of the multistate characters are appropriate for linear orderings, but no alternate orderings were suggested. Oddly, a few binary characters (28, 30, 33, 35-36,

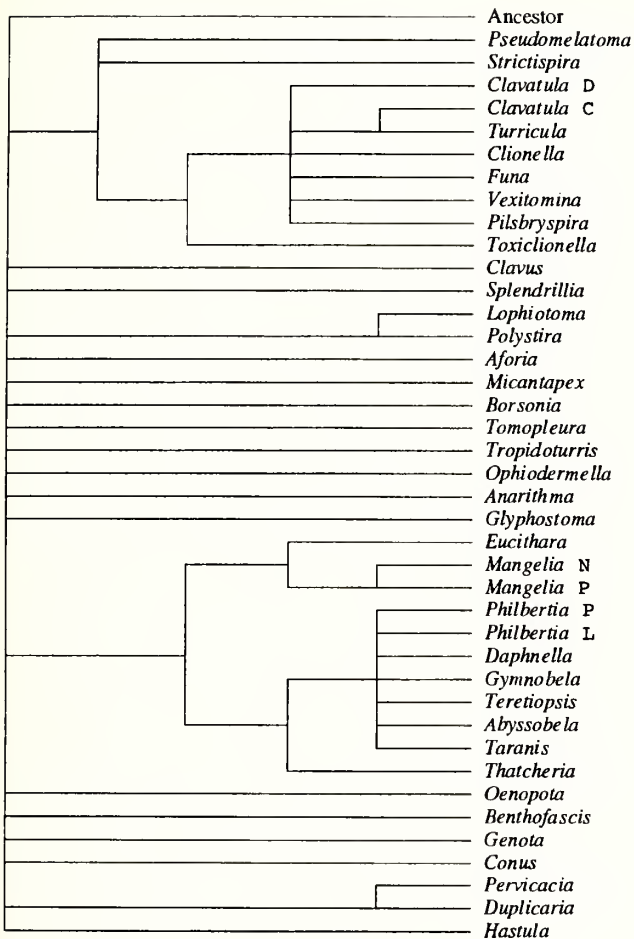


Fig. 4. Analysis II (excluding *Benthobia*); strict consensus of 32,700 trees, length 187, CI = 0.294, RI = 0.617, HI = 0.706, RC = 0.182. Search history: replicate 1 (seed = 581470058), 31,351 trees found (length = 187); replicate 2 (seed = 426658209), MAXTREES limit (32,700) hit while swapping on tree #31538, 1,349 additional trees found (length = 187). Total number of rearrangements tried = 764211632, time used = 24:40:51.

41-42), which are by definition unordered, appeared on each list.

The discrepancies in the lists of unordered characters raise the possibility that through some error the published matrix is not the version of the matrix that was analyzed to produce the TKS tree. Taylor *et al.* (1993: 152) referred to making "small adjustments to the data set" as they explored their data, and Taylor and Kantor (pers. comm.) stated that they tried various scorings of characters and experimented with both ordered and unordered characters. Assuming that all the characters were unordered (and equally weighted), I used MacClade to determine the length of the TKS tree, which, although it is a consensus tree, is fully resolved. It does indeed have the stated length of 189 steps. Thus the published matrix is consistent with the pub-

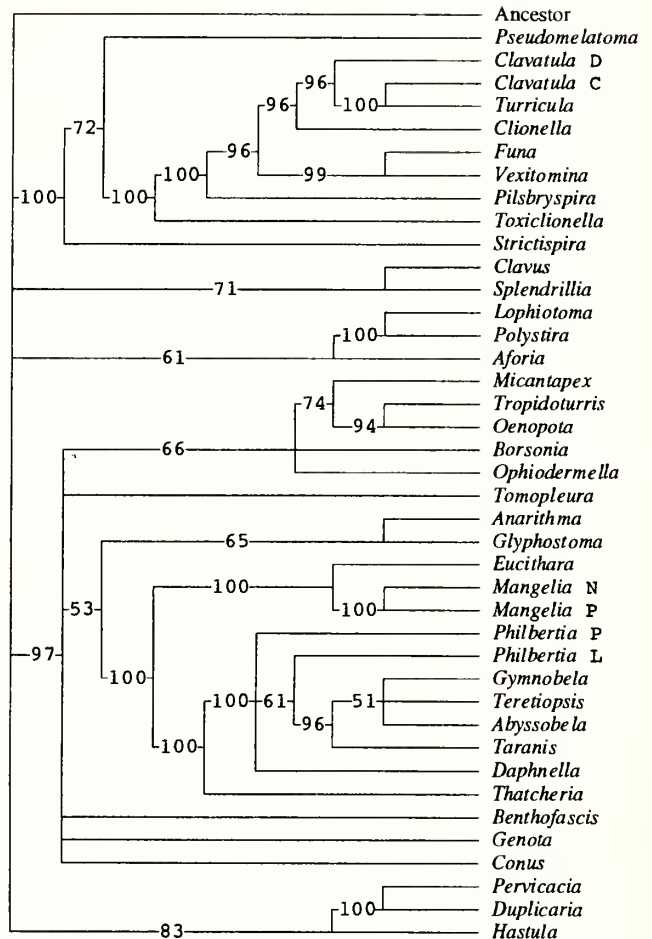


Fig. 5. Analysis II (excluding *Benthobia*); 50% majority-rule consensus of 32,700 trees of length 187.

lished tree, and with the assumption that all characters were unordered.

Exclusion of the outgroup

Analysis I (original data matrix) found 3,149 trees of length 193 (Fig. 2-3). Taylor *et al.* (1993: 152) reported "over 900" trees of length 189, four steps shorter, for this matrix. Their consensus tree (Fig. 1), however, omits *Benthobia*, which was selected as the outgroup being "the most primitive non-conoidean neogastropod known" (1993: 152). In all trees of length 193, *Benthobia* fell within the ingroup, usually grouping with the Pervicaciinae. Taylor and Kantor (pers. comm.) stated that they excluded *Benthobia* from the analysis because of this behavior. Thus the analysis presented by Taylor *et al.* corresponds to Analysis II herein.

I tried forcing *Benthobia* to stay in outgroup position, using the topological constraints option of PAUP. A heuristic search as described above resulted in 32,700 trees

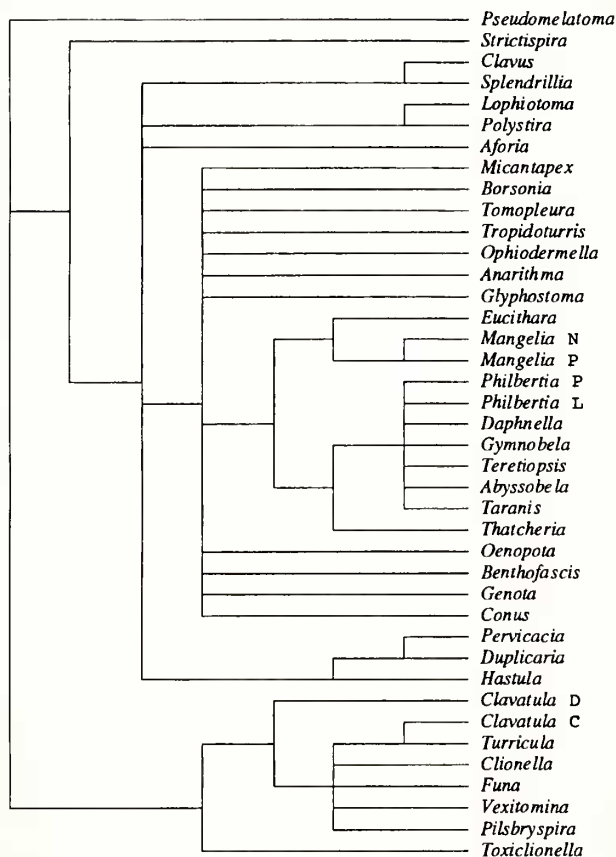


Fig. 6. Analysis III (excluding *Benthobia* and hypothetical ancestor); strict consensus of 10,490 trees, length 182, CI = 0.302, RI = 0.622, HI = 0.698, RC = 0.188. Search history: replicate 1 (seed = 1): 10,490 trees found (length = 182); replicate 2 (seed = 1459270432): MAXTREES limit (32,700) hit while swapping on tree #16,743, 22,210 non-minimal trees (length = 183) discarded. Total number of rearrangements tried = 403556096, time used = 16:25:50.

of length 194, one step longer than without the constraint. The strict consensus and majority rule consensus trees were quite similar to those for Analysis III (Figs. 6-7), in which the outgroups were excluded, but slightly more resolved because of small differences in support for a few clades (*e. g.* 100% versus 96%, 53% versus 47%) and so are not shown here.

Shortest trees

Analysis II (with *Benthobia* excluded) yielded 32,700 trees of length 187, two steps shorter than those found by Taylor *et al.* I ran the matrix several times using different starting seeds. In my analyses, runs always terminated because PAUP's maximum limit of 32,700 trees was reached. This generally took ca. 24 hr. In some cases, trees of length 187 were found in only a few minutes; in others, the shortest trees found before memory overflowed were length 188. In no replicates were trees of length 189

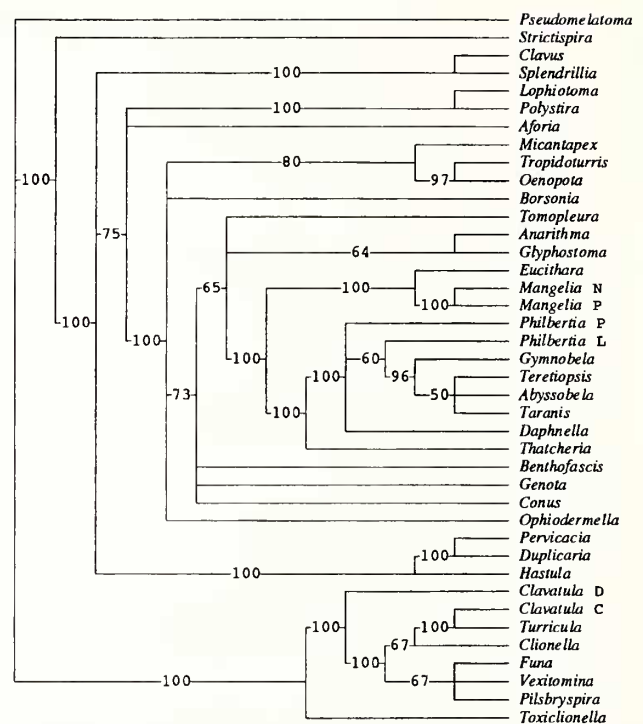


Fig. 7. Analysis III (excluding *Benthobia* and hypothetical ancestor); unrooted, 50% majority-rule consensus of 10,490 trees of length 182.

retained as the shortest trees. Taylor and Kantor (pers. comm.) told me that their runs terminated when the computer they used ran out of memory. This explains why Taylor *et al.* found trees of length 189 rather than 187 or 188 and why they found only 900+ trees rather than many thousands of trees: they simply did not have enough computing power. This should have been stated in the article, however, which otherwise gives the impression that the heuristic search routine was completed. Because Taylor *et al.* did not state the starting conditions of their analysis (*e. g.* MAXTREES or other search settings) or the ending conditions, their results could not be reproduced.

HYPOTHETICAL ANCESTOR

Because there is no obvious sister group for Conoidea, Taylor *et al.* (1993: 152) used a hypothetical ancestral taxon "consisting of the underived states, where known, of the characters used in the analysis." Construction of such a hypothetical ancestor is not unusual. A common procedure is to consider a variety of potential outgroups. If only one state occurs in the possible outgroups, the polarity is clear (Donoghue and Cantino, 1984). Taylor *et al.* apparently applied this type of reasoning in some cases (*e. g.* for accessory salivary glands; 1993: 142), but in many cases did not state how they made decisions about polarity. In other cases, the reasons they gave are known to be invalid,

Table 1. Consensus of consensus trees: clades co-occurring in each of the six consensus trees (Figs. 2-7) and the TKS tree (Fig. 1). (Trees from Anal[ysis] I, II, III; MRC, majority rule consensus tree; SC, strict consensus tree).

TKS Clade	Clade shared by tree in:					
	Fig. 2	Fig. 4	Fig. 6	Fig. 3	Fig. 5	Fig. 7
	Anal I SC	Anal II SC	Anal III SC	Anal I MRC	Anal II MRC	Anal III MRC
1	x	-	x	x	x	x
2	-	-	-	-	-	-
3	-	-	x	-	x	x
4	-	x	x	x	x	x
5	-	-	-	-	-	-
6	-	x	-	x	x	-
7	-	-	-	-	-	-
8	-	-	-	-	-	-
9	x	x	x	x	x	x
10	x	-	x	x	-	x
11	-	-	-	x	-	x
12	x	x	x	x	x	x
13	-	-	-	x	-	x
14	-	-	-	-	-	-
15	-	-	-	-	-	x
16	-	-	-	x	x	-
17	x	x	x	x	x	x
18	-	-	x	x	x	x
19	-	-	-	-	-	-
20	-	-	-	-	-	-
21	-	-	-	-	-	-
22	-	-	-	-	-	-
23	-	-	-	-	-	-
24	-	-	-	x	x	x
25	-	-	-	-	-	-
26	-	-	-	-	-	-
27	-	-	-	-	-	-
28	-	-	-	-	-	-
29	x	x	x	x	x	x
30	x	x	x	x	x	x
31	x	x	x	x	x	x
32	x	x	x	x	x	x
33	x	x	x	x	x	x
34	-	-	-	-	-	-
35	-	-	-	-	-	-
36	-	-	-	x	x	x
37	-	-	-	x	-	x
38	-	-	-	-	-	-
Total shared clades	10	10	13	19	16	19

such as the three criteria they explicitly mentioned (1993: 132). These are occurrence of character states (1) in taxa with the least derived states of other characters, (2) in most of the subfamilies of Turridae (*i. e.* common equals primitive), and (3) in distant rather than immediate outgroups (some members of Archaeogastropoda or "Mesogastropoda" rather than other Neogastropoda).

The first criterion assumes that primitive character states are correlated, but as Stevens (1980: 334) noted,

"Correlations do not necessarily indicate anything about the evolutionary polarity of the characters states involved ... character states may be associated in various ways: all primitive, all derived, or mixed ..." Of the second criterion, Stevens (1980: 335) stated, "the frequency of any character state in a group depends on the subsequent evolutionary history of the lineage with that state and is independent of the evolutionary polarity of that state." Thus a primitive character might be rare if it belongs to a lineage that has not diversified or has suffered much extinction. A derived character might be common if it arose early in the history of a clade. The third criterion ignores that the character states of distant outgroups cannot override the states in closer outgroups; at best they can render polarity ambiguous with regard to the ingroup (Maddison *et al.*, 1984: fig. 3). Also, at least in some cases, Taylor *et al.* applied the first two criteria within the ingroup, rather than doing outgroup comparisons (*e. g.* buccal mass position; 1993: 132).

Because of doubt about the scoring of character states for the hypothetical ancestor, I tried running the analysis without it (and without *Benthobia*) (Analysis III), finding 10,490 trees of length 182. Curiously, the consensus trees for these (Figs. 6-7) have more clades in common with the TKS tree than the consensus trees when the hypothetical ancestor was included: 13 versus ten (strict); 19 versus 16 (majority rule) (Table 1). In particular, clade 18, which groups Conidae with a subset of Turridae, appears in the strict consensus.

CONSENSUS OF THE CONSENSUS TREES

The strict consensus trees (with and without the outgroups) each share only ten to 13 clades with the TKS tree (Table 1), which has a total of 38 clades. Only eight clades are shared by all three strict consensus trees and the TKS tree (node numbers in parentheses): Clavatulinae (part) + Crassispirinae + Zonulispirinae (9); *Clavatulula caerulea* + *Turricula* (12); Turridae (17); Mangeliinae + Daphnellinae + Taraninae (29); Mangeliinae (30); *Mangelia* (31); Daphnellinae + Taraninae (32); and *Philbertia* + *Daphnella* + *Gymnobela* + *Teretiopsis* + *Abyssobela* + *Taranis* (33). One clade appears in all three strict consensus trees that does not appear in the TKS tree: Clavatulinae (all) + Crassispirinae + Zonulispirinae.

Only 13 of the 38 clades are shared by all three majority-rule consensus trees, those in the strict consensus trees, listed above, and: Drilliidae (1); Pervicaciinae (4); Conidae *sensu* Taylor *et al.* (18); *Anarithma* + *Glyphostoma* (24); and *Gymnobela* + *Teretiopsis* + *Abyssobela* + *Taranis* (36). Seventeen clades supported by the Taylor *et al.* analysis are not supported by any of the trees presented herein: 2, 5, 7, 8, 14, 19, 20, 21, 22, 23, 25, 26, 27, 28, 34, 35, and 38.

Taylor *et al.* (1993: 152) did not state the level of

support for any of the nodes in their consensus tree, saying instead "most of the branches are supported in 75-100% of the trees." Because of this omission, it is not possible to tell where disagreement is significant. Lack of support in my analysis for a node supported in only 55% of their trees would not be surprising; lack of support for a node supported in 100% of their trees would be more interesting. The 17 nodes contradicted by my analysis average only 1.8 characters per node (Taylor *et al.*, 1993: table 4), whereas the 12 nodes supported by all three of my consensus trees average 3.3 characters per node. The mapping of characters to nodes is often ambiguous, however, and many alternative mappings to the ones in their table 4 exist. For example, character 3(1) was mapped to node 3, with loss in *Pervicacia*. An alternate mapping is independent gain in *Hastula* and *Duplicaria*.

CHARACTERS

Character mappings

In addition to some characters in table 4 of Taylor *et al.* having alternate mappings, some mappings are simply incorrect. Kohn and McLean (1994) noted that character state 39(0) at node 27 (*Benthofascis* + *Conus*) should be mapped at node 26 instead, because it is present in *Genota*. Actually, 39(0) is a primitive state inherited from the root of the tree. State 39(1) (teeth on the outer lip) evolved at nodes 24 and 33 and in *Eucithara*; it was lost at node 36. There is no need to map 39(0) elsewhere in the tree. Similarly, character states 20(1), 35(0), and 38(1), mapped to node 1 (Drilliidae), are actually basal to the conoideans. Also at node 1, *Clavus* has state 7(2) not 7(1). Thus four of the five synapomorphies attributed to Drilliidae in Taylor *et al.*'s table 4 do not map to that node (in the given topology). The remaining character state, 37(0), has an ambiguous mapping, as node 3 has the same state, which thus could be basal, changing to 37(1) at node 5.

Parallelism

The majority of characters (77%) that Taylor *et al.* used are from a single organ complex, the foregut. Any classification based primarily on characters from one system is likely to be misled by parallelisms. Cladograms based on characters from many organ systems are less likely to be misleading (Davis, 1979: 9). Taylor *et al.* (1993: 151) noted:

many of the morphological trends in the Terebrinae involve partial to total loss of the foregut organs ...thus many of the characters were recorded as missing. In our earlier attempts at cladistic analysis, terebrid species tended to appear in rather disparate positions on the cladograms. Consequently, we have

used only three species to represent the Terebrinae and Pervicaciinae, the taxa being the least-derived known for each group.

Inclusion of characters from the reproductive, circulatory, excretory, and respiratory systems might have overridden the problem caused by the supposed parallel losses in the Terebridae. Paradoxically, understanding of the evolution of the foregut organs requires study of the other organ systems - they cannot be studied in isolation. The hope is that homoplasy in any given system will be more than balanced by the overall phylogenetic signal in combined analysis across systems. An excellent example of this is *Benthobia*. Because of homoplasious characters in foregut anatomy, it was pulled into the ingroup, but the overall anatomy and morphology place it securely with the Pseudolividae (Kantor, 1991; see also Bouchet and Warén, 1985). The single species of *Conus* included in the analysis might have been pulled into Turridae because of parallelisms, just as *Benthobia* was pulled into Conoidea.

Choice and scoring of characters

Some of the ten non-foregut characters analyzed were overly simplified. For example, the division of shell form into "fusiform," "coniform," "turreted," "terebriform," and "rounded" is simply unworkable in the continuum of shapes that occur among the more than 4,000 living species of conoideans, especially because quantitative definitions of these terms were not given (Taylor *et al.*, 1993: 162). Number of protoconch whorls (< 2, > 2) is also an arbitrary division of a continuum, although it tends to correlate with developmental type. Sculpture of the protoconch (absent or weak versus present) combines many disparate types of sculpture as a single character state.

Kohn and McLean (1994) noted that potentially useful shell characters were excluded, such as the resorption of the inner shells whorls found in *Conus* and *Benthofascis*, which Taylor *et al.* mentioned (1993: 155), but did not include in their matrix. Taylor (1994: 435) stated, "We considered, but did not include this character in the cladistic analysis. Its inclusion would have made no difference to the structure of the cladogram except to add another apomorphy at the node of *Benthofascis* and *Conus*." This clade, however, is not supported by any of the consensus trees presented herein. Inclusion of the character might well have resulted in support for this clade.

There are also some inconsistencies in the scoring of foregut characters. Character 15 (septum dividing anterior and posterior areas of the rhynchocoel) was listed as present in *Philbertia purpurea*, *Daphnella*, *Pervicacia* and *Duplicaria* in Taylor *et al.*'s table 3, but a "probably homologous septum" reported in *Thatcheria* (1993: 129) was not scored in the matrix. For Character 26, *Strictispira paxillus*

(Strictispiridae) has state 1 (Taylor *et al.*, 1993: table 3), which was stated to occur only in Pseudomelatomidae (1993: 136), and *Hastula bacillus* was scored “?” but has state 2 (1993: table 2). For Character 33, *Pseudomelatoma*, *Splendrilla*, *Toxiclionella*, and *Lophiotoma* were scored as having unfused odontophoral cartilages in table 3, but stated to have fused cartilages on p. 133.

CHOICE OF TAXA

Although one of the major conclusions of the study was that some subfamilies of Turridae should be transferred to Conidae, only a single species of *Conus* from among the more than 500 living species was included in the analysis (two species were studied [Taylor *et al.*, 1993: table 1]). The study thus did not provide evidence that *Conus* is monophyletic. Similarly, six of the subfamilies included in the analysis were represented by only one species each. Again, no evidence was provided that these groups are monophyletic, yet two, Pseudomelatomidae and Strictispiridae, were elevated to familial rank. Other taxa studied were excluded from the cladistic analysis, in the case of some Terebridae explicitly because they did not group as expected. Many other species listed in Taylor *et al.*'s table 1 did not appear in their table 3, but no explanation was given for their exclusion. One hopes that they were excluded because of insufficient data, or because character scores did not differ from those of included species, rather than for cladistic misbehavior.

CLASSIFICATION

The classification that Taylor *et al.* introduced does not follow the structure of their cladogram (Fig. 1), as noted by Kohn and McLean (1994): Turridae, Clavatulinæ, and Clathurellinæ are polyphyletic, and Crassispirinæ, Conorbinae, and Daphnellinæ are paraphyletic. Taylor *et al.* stated (1993: 157), “Information from taxa not included in the cladistic analysis (mainly radular characters) has also been used in constructing the classification.” Presumably these taxa were not included because other data on their foregut anatomy was not available. Unfortunately, inclusion of such information, however relevant, adds another layer of irreproducibility to the analysis. Such data might be used to choose between equally parsimonious trees, but beyond that, there seems little justification for their use.

Taylor *et al.*'s classification conflicts with their tree because it is in part conservative. An alternative classification more consistent with the tree would introduce new subfamily names for parts of Clavatulinæ, Clathurellinæ, and Crassispirinæ, and synonymize Conorbinae with Coninæ, and Taraninæ with Daphnellinæ. That Taylor *et al.* refrained from naming new taxa is appropriate, given the preliminary nature of the data. This conservatism is at odds, however, with the elevation of Strictispiridae and

Pseudomelatomidae to family level, which renders Turridae polyphyletic instead of paraphyletic.

The essential conflict of the tree is that Conidae falls within Turridae. The solution that Taylor *et al.* adopted (transferring some turrid subfamilies to Conidae) left Turridae paraphyletic (ignoring for the moment the rank of Strictispiridae and Pseudomelatomidae). This is no better than accepting the traditional classification, in which Turridae might also be paraphyletic. At several points Taylor *et al.* stressed the limitations of their analysis. They noted that “small adjustments to the data set produced rather large changes in tree topography [*sic*] and the number of alternative trees generated” (1993: 152), uncertainty about outgroups (p. 152), and inadequate sampling of taxa (p. 150). In view of these uncertainties, it is not clear why they introduced a new classification - producing the data and cladogram would have been enough.

CONCLUSIONS

The results of Taylor *et al.* (1993) cannot be reproduced from their stated methods. The trees they reported are not minimal trees because the analysis they performed terminated prematurely, being limited by memory of their computer. Further problems arise from omission of the stated outgroup, *Benthobia*, from the cladistic analysis, incorrect character mappings, and conflicts between text and data matrix. The classification that Taylor *et al.* introduced does not follow the structure of their cladogram, taking into account data from taxa not included in the cladistic analysis. This adds further layers of irreproducibility to the results.

Taking the data matrix as given, fewer than half of the clades they found were supported by my reanalysis. The matrix, however, is probably not a reliable basis for a phylogenetic analysis. Most of the characters used were from a single organ complex, the foregut, making it likely that the parsimony analysis was misled by parallelism, as evidenced by the pseudolivid outgroup, *Benthobia*, being pulled into the ingroup. Also, some of character states of the hypothetical ancestor were determined by unreliable methods such as ingroup comparison, so the polarities of characters were not well established. Addition of outgroup and ingroup taxa, rescoring of some characters, and of the hypothetical ancestor, and addition of characters from other organ systems would undoubtedly further modify the results.

Nonetheless, I did find support for some aspects of the Taylor *et al.* analysis, taking the data matrix as given. Mangeliinæ + Daphnellinæ + Taraninæ (node 29), and subsets thereof are supported in the strict consensus trees, as is Turrinæ, and Clavatulinæ + Crassispirinæ +

Zonulispirinae (9), with *Toxiclionella* pulled in also, making Clavatulinae paraphyletic rather than diphyletic. Most interesting is that node 18, Conidae *sensu* Taylor *et al.* (Conidae + Clathurellinae, Conorbinae, Oenopotinae, Mangeliinae, Daphnellinae, and Taraninae) appears in all three majority-rule consensus trees. Support for this clade is not unequivocal, however, as it does not appear in two of the strict consensus trees. Given the limitations of the character data and taxon sampling, it is yet possible that Conidae and Turridae will prove to be two separate clades. The single *Conus* species included in the analysis could well have been pulled into Turridae because of parallelisms, just as *Benthobia* was pulled into Conoidea. Malacologists will be justified in retaining the traditional classification, until more robust evidence for transferring turrid subfamilies to Conidae and for elevating Drilliidae, Pseudomelatomidae, and Strictispiridae to familial status is produced.

Given the authors' cautions about the preliminary nature of their analysis, their introduction of a new classification was premature. The monumental achievement of presenting the anatomical descriptions, assembling the data matrix, and presenting a preliminary tree would have been sufficient. Certainly it is much better to have this data available now than to wait five or ten years while the authors tackled other taxa and other organ systems to produce a better-supported phylogeny. One advantage of cladistic over traditional methods is that intermediate results can be presented without the need to introduce a new classification. Once a new classification is introduced, inevitably some will adopt it, even if it is likely soon to be superseded. For example Turgeon *et al.* (1998) adopted Taylor *et al.*'s new classification of Conoidea.

I note in closing that it was not the introduction of the new classification itself that spurred this reanalysis but that other workers were adopting a classification that I thought likely to be incorrect. Thus, the new classification did draw attention to ideas that have stimulated scientific discourse. Perhaps it has served its purpose after all.

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